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Effects of environmental hypoxia on oxygen consumption rate and swimming activity in juvenile white sturgeon, *Acipenser transmontanus*, in relation to temperature and life intervals

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Synopsis

Routine oxygen consumption rates (MO_2) and swimming activity rates of juvenile white sturgeon were determined using closed respirometers at life-interval-appropriate temperatures: 10° C (0.2 g mean wet weight), 16° C (1.9 g mean wet weight), and 20° C (63.1 g mean wet weight) under normoxic ($PO_2 > 140$ mmHg) and moderately hypoxic ($PO_2 = 80 \pm 5.0$ mmHg) water conditions. At all temperatures and body sizes, hypoxia significantly depressed ($p < 0.05$) MO_2 (57% mean reduction) and swimming activity (70% mean reduction). Overall mean MO_2 was 228 μg O_2 g^{-1} wet weight h^{-1} (normoxia) and 99 μg O_2 g^{-1} wet weight h^{-1} (hypoxia). Thus, juvenile white sturgeon appear to decrease overall energy expenditures (hypometabolism) during hypoxia via reductions in spontaneous swimming activity. This is a life style that may increase survival during widespread or prolonged environmental hypoxia.

Introduction

The white sturgeon, *Acipenser transmontanus*, is a semianadromous, demersal fish that inhabits three major river systems in the Pacific Northwest region of North America: the Sacramento, the Fraser, and the Columbia (Stevens & Miller 1970, Kolhorst 1980, Bergen et al.[1], Lane 1991, Moyle & Cech 1996). The northern California population of adult white sturgeon remains year-round in the Sacramento-San Joaquin River systems and associated San Francisco Bay estuarine system.[1] While most of the spawning occurs upstream of the confluence (termed the 'Delta') of the two major rivers (Stevens & Miller 1970), adult fish concentrate in the brackish water of Suisun and San Pablo Bays to feed (Kolhorst et al. 1991). They also use the estuary as a nursery area for their young([1]).

Environmental hypoxia can occur in regions of the estuary due to stagnation caused by inadequate mixing of surface water or, from relatively high biological oxidative activity (e.g., associated with muddy bottom habitats; Laws 1981, Moyle & Cech 1996). Burggren & Randall (1978) reported that sub-adult white sturgeon (mean weight 0.95 kg) decrease their respiratory metabolic rate (hypometabolism, through measurements of oxygen consumption rate) when exposed to environmental hypoxia.

In order to decrease their overall metabolism, there must be a reduction of activity or some other significant component(s) of an animal's total ener-

[1] California Department of Fish and Game. 1992. Draft for the State Water Resources Control Board, Water Rights Phase of the Bay-Delta Estuary Proceedings. 13 pp.

gy budget (Jobling 1993). A major component of metabolic energy expenditure can be swimming activity (Fry 1971). Burggren & Randall (1978) did not measure volitional swimming activity associated with the sturgeon's metabolic rates and their metabolic data on white sturgeon contrast with those for other sturgeon species. For example, juvenile Adriatic sturgeon, *Acipenser naccarii* (Randall et al. 1992) and adult Siberian sturgeon, *Acipenser baerii* (Nonnotte et al. 1993, Maxime et al. 1995) do not decrease MO_2 during hypoxia. Cech et al. (1984) described significantly reduced juvenile white sturgeon growth rates under hypoxia, probably resulting from reduced feeding activity. Overall, there is a lack of information on effects of environmental hypoxia on resting routine metabolic level in juvenile white sturgeon.

Our objective was to measure oxygen consumption rates and volitional swimming activity rates of white sturgeon at a low dissolved oxygen concentration and at environmental temperatures matching the habitats of age-0 fish during their seasonal development in the Sacramento River. Based on the observations and results of Burggren & Randall (1978) and Cech et al. (1984), we hypothesized that exposure to low dissolved oxygen would reduce routine MO_2 in sturgeon, possibly via reductions in spontaneous swimming activity. Information concerning swimming activity during hypoxia is essential for our understanding of the environmental requirements and limitations of white sturgeon.

Materials and methods

Fish source and maintenance

Sibling white sturgeon (n = 250; one week after hatching) were obtained from the University of California, Davis (UCD), Aquaculture and Fisheries Program facility and transported to the UCD Fish Ecophysiology laboratory where they were maintained in a 1 m diameter, flow-through, fiberglass tank supplied with unchlorinated well water (10° C). They were kept on a natural photoperiod and fed ad libitum rations (Silvercup trout pellets) twice a day. Feces and uneaten food were siphoned out of the tanks daily. Food was withheld 24 h before experimentation.

Acclimation and grow-out protocol

Data were collected from three different size groups of age 0 white sturgeon at size-appropriate temperatures. The small fish (n = 30; 0.2 ± 0.0 g mean wet weight; 2.0–2.5 cm TL) were acclimated to 10° C because this is near the lower temperature limit for spawning sturgeons and subsequent early development in upper river habitats (McCabe & Tracy 1994, Parsley et al. 1993, LaHaye et al. 1992). Hypoxia effects on oxygen consumption rates were determined both in the normoxia-hypoxia and the hypoxia-normoxia sequences. Fish not used for the 10° C experiments were slowly acclimated (<1° C 48 h^{-1}) and allowed to grow at 16° C. These medium-size fish (n = 105; 1.9 ± 0.1 g mean wet weight; 4.0–5.0 cm TL) fish were acclimated at 16° C because this temperature approximates the water temperature encountered by juvenile sturgeon before they enter sloughs in late spring (Lane 1991). Fish not used in these experiments were slowly acclimated to 20° C (< 1° C 48 h^{-1}) and allowed to grow until use in subsequent experiments. These large juveniles (n = 24; 63.1 ± 4.0 g mean wet weight; 11.0–14.0 cm TL) were acclimated at 20° C to stimulate shallow habitats of late summer (California Dept. Water Resources[2]) that have the wider temperature ranges white sturgeon tolerate as they develop (Buddington 1989).

Experimental procedures

Routine oxygen consumption rate (MO_2) was measured on individuals of the three size groups of juvenile fish using closed respirometers (see Cech 1990). Replicate (4–8) glass respirometers were situated in an accerated and temperature-controlled fiberglass water bath maintained at the experimental temper-

[2] California Department of Water Resources. 1976. Sacramento-San Joaquin Delta Water Quality Surveillance Program, Volume 1. State of California.

ature (10, 16, or 20° C). Temperatures were maintained (± 0.5° C) using water chillers balanced with submersible heaters connected to a proportional controller (YSI Model 72). Each fish was randomly selected from a temperature-controlled holding tank (10, 16, or 20° C), gently netted, weighed in a tared container of water, and transferred to a bubble-free respirometer. The small and medium sized fish were placed into 4 cm diameter, 9 cm long, 0.09 l respirometers, and the large fish were placed into 13 cm diameter, 24 cm long, 3.9 l respirometers. Each respirometer housed one fish and all respirometers were partially shielded with black plastic in order to reduce stress associated with movements of fish in adjacent respirometers, and the activities of the investigators.

The fish were allowed at least 2 h to recover from handling, while tank water circulated through the respirometers, prior to data collection.

Each experiment lasted approximately 4 h and was divided into three continuous periods; a control period, a transition interval, and a treatment period. After the 2 h respirometer acclimation period (water PO_2 > 140 mm Hg), the fish were subjected to 0.5 h, normocapnic exposure (control) that approximated air-saturation conditions (160 > water PO_2 > 140 mm Hg). During the last minute of the control period, a 1.0 ml water sample was taken from each respirometer for PO_2 determination. The control period was followed by a 1 h transitional period that began with an acute, uniform decrease of water PO_2 (60 torr). Hypoxia (PO_2 = 80 mm Hg ± 5.0 mm Hg) was established (within 5 minutes) and maintained by counterflows of tank water and nitrogen gas, delivered via diffuser stones, in a gas stripping column (Fry 1951) of PVC construction that supplied the respirometers. After the transition interval, the treatment period, a 0.5 h hypoxic exposure, was initiated. During the last minute of the hypoxic period, a 1.0 ml water sample was taken from each respirometer for PO_2 determination.

All fish groups were subjected to the normoxia-hypoxia sequence (above). We also subjected a groups of small fish (0.2 ± 0.0 g mean wet weight) to a hypoxia-normoxia sequence. The protocol was similar to the normoxia-hypoxia sequence except that for these fish, the control period was a 0.5 h hypoxic exposure (following a 2 h acclimation period in hypoxic water; PO_2 = 80 mm Hg ± 5.0 mm Hg, 10° C). During the last minute of the hypoxic period (control), a 1.0 ml water sample was taken from each respirometer for PO_2 determination. An air flow was substituted for the nitrogen to get the system to normoxia during the 1 h transition period. The treatment period was a 0.5 h normoxic exposure and during the last minute of this period, a 1.0 ml water sample was taken from each respirometer for PO_2 determination.

During each experiment, one chamber was always left empty to serve as a blank for microbial respiration (Cech 1990). In between experiments, respirometers, tubing, and all associated equipment were cleaned with a mild bleach solution, rinsed, and flushed for at least 24 h prior to use.

A video camera was situated above the respirometers to record swimming activity (horizontal movement) during normoxia and hypoxia. The index of volitional swimming activity (linear movements within respirometers; cm h^{-1}) was subsequently estimated from the video tapes by counting the number of lines (painted on each respirometer) crossed as a fish swam along the long axis of the respirometer. Some fish occasionally swam in dimensions other than those used to quantify activity (e.g., side-to-side movements), but these movements were infrequent and not included in the determination of activity.

Water PO_2 was measured with a thermostatted Radiometer PHM71/D616/E5046 oxygen analyzer system and converted to oxygen concentrations (µg O_2 l^{-1}) using the nomogram of Green & Carritt (1967). Resting routine MO_2 (µg O_2 g^{-1} h^{-1}) were calculated from:

$$MO_2 = (CO_2i - CO_2f)\ (V)g^{-1}\ t^{-1},$$

where CO_2i = initial water oxygen content (µg), CO_2f = final water oxygen content (µg), V = respirometer volume (l), g = mass of fish (g), and t = time (hours). Microbial respiration (MO_2 of blank respirometers) corrections were applied to calculated MO_2 data for the fish. The model [MO_2 = constant + temperature + logwt. + (temperature * logwt)] was used to estimate the interaction effect

between acclimation temperature and fish mass on MO_2.

Statistical analyses

MO_2 and activity results are expressed as means ± SEM, and comparisons at the same or between different acclimation temperatures were made using either t-tests or multiple comparisons analysis of variance (ANOVA; Sigmaplot statistical software). The interaction effect between fish mass and acclimation temperature on MO_2 was estimated using analysis of covariance (ANCOVA; SYSTAT statistical software; covariates were log weight and temperature). Treatments were considered significantly different if $p < 0.05$.

Results

Effects of hypoxia on swimming activity and metabolism

Mean swimming activity (cm h^{-1}) decreased significantly ($p < 0.05$) during hypoxia in all fish, with an overall mean decrease of 78%. Mean decreases for small, medium, and large fish during hypoxia, were 82%, 65%, and 88%, respectively, (Figure 1a). The decrease in swimming activity associated with hypoxia, was independent of exposure sequence. The small fish subjected to the hypoxia-normoxia sequence were nearly motionless during hypoxia (7.3 ± 1.5 cm h^{-1}) and then during normoxia, volitional swimming activity increased significantly (33.4 ± 3.0 cm h^{-1}). Metabolic responses to hypoxia closely matched the swimming responses in juvenile white sturgeon. All fish significantly ($p < 0.05$) decreased MO_2 during hypoxia, compared with normoxic MO_2 data for the same size fish at the same temperature (Figure 1b). Overall mean MO_2 was 228 µg O_2 g^{-1} wet weight h^{-1} (normoxia) and 99 µg O_2 g^{-1} wet weight h^{-1} (hypoxia). MO_2 for the small, medium, and large fish decreased by 78%, 38%, and 22%, respectively, showing a trend of reduced metabolic response magnitude with hypoxia, as the sturgeon grew larger and occupied warmer

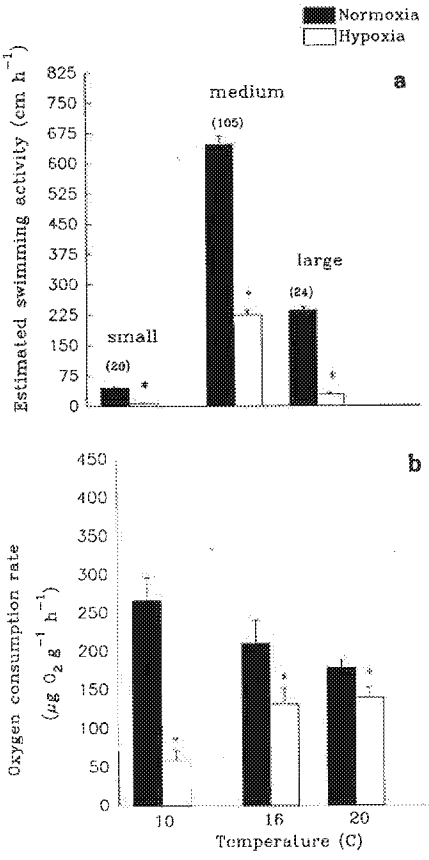

Figure 1. a – Mean ± SEM estimated swimming activity and *b* – oxygen consumption rate of juvenile white sturgeon (10° C, 0.2 ± 0.0 g mean wet weight, 16° C, 1.9 ± 0.1 g mean wet weight, and 20° C, 63.1 ± 4.0 g mean wet weight) during normoxia and hypoxia. Asterisks (*) = significantly different from normoxic controls at the same temperature ($p < 0.05$), and n are given in parentheses.

habitats. The exposure sequence (hypoxia-normoxia) did not significantly alter this result. The small fish subjected to the hypoxia-normoxia sequence (10° C) showed reduced MO_2 (13 ± 5.0 µg O_2 g^{-1} wet weight h^{-1}) during hypoxia which increased significantly to 50 ± 13.0 µg O_2 g^{-1} wet weight h^{-1} during normoxia.

The influence of body weight and temperature on MO_2

As expected from the experimental design, after adjusting for the effects of body size and temperature differences between groups, there was a significant ($p < 0.001$; ANCOVA) interaction between

acclimation temperature and fish body mass on MO_2 in white sturgeon. Oxygen consumption increases as fish get larger and/or move into warmer water.

Discussion

The metabolic and swimming activity responses to short-term hypoxia displayed by white sturgeon were very consistent across body sizes and temperatures, suggesting that the decreased locomotory pattern may have evolved to survive chronic and widespread environmental hypoxia. Historically, the Sacramento-San Joaquin Delta was probably characterized by large marshy areas of stagnant water, especially during the dry summer and autumn period when age-0 white sturgeon would be present (Moyle 1976). Such a response would not seem to have selective value if hypoxia was more localized and could be easily avoided with increased activity to escape the hypoxic zone. Similarly, aquatic surface respiratory activity (inspiring water at the air-water interface, Kramer 1978) would likely expose these small fish to avian predators. The reduction in volitional swimming activity during hypoxia has been documented in hypoxic Atlantic cod, *Gadus morhua* (Schurmann & Steffensen 1994), and during anoxia in crucian carp, *Carassius carassius* (Nilsson et al. 1993), presumably as an 'energy-saving' survival life style for long-term hypoxic exposure (Satchell 1971). Nilsson et al. (1993) suggest that a considerable amount of energy used by a spontaneously active fish can be attributed to locomoter activity. Hypoxia-induced reductions in spontaneous swimming reduce energy expenditures (hypometabolism) during prolonged hypoxic exposure and may increase survival, provided the fish does not succumb to starvation, predation, or disease. In contrast, increased swimming activity is displayed by guppies, *Poecilia reticulata* (Weber & Kramer 1983), the sand goby *Pomatoschistus minutus* (Petersen & Petersen 1990), and brook charr, *Salvelinus fontinalis* (Tang & Boisclair 1995) during moderate hypoxia. This response may constitute escape attempts from a more localized hypoxic zone.

The hypometabolic response to hypoxia may be innate in white sturgeon. Our fish were significantly smaller and younger than those used by Burggren & Randall (1978) however, the metabolic response (decreased MO_2) to hypoxia was identical. While the reduced MO_2 reported for white sturgeon by Burggren & Randall (1978), was not attributable to reduced volitional activity, it may have resulted from shifts in cardiovascular (cardiac output and regional blood flow distribution) performance initiated to safeguard O_2 transport/delivery to 'vital tissues'. In the present study, the swimming and oxygen consumption decreases shown by the small juvenile white sturgeon, regardless of the normoxia-hypoxia or the hypoxia-normoxia sequence, demonstrate that they resulted from the hypoxic condition and not some other effect, e.g., prolonged periods in the respirometer. This is significant and supports our hypothesis that the adaptive profile for white sturgeon's includes an ability to survive in hypoxic waters by remaining inactive (hypometabolism). Currently, we are uncertain as to whether the decrease in swimming activity caused the decreased oxygen consumption rate (by reducing metabolic O_2 demand) or, if the delivery of oxygen to skeletal muscle was inadequate to sustain swimming activity. Further research is needed to address these issues and to investigate the significance of cardiovascular and regional blood flow changes associated with hypoxia in white sturgeon.

In the present study, juvenile sturgeon at 10° C did not exhibit a compensatory increase in oxygen consumption rate after a return to normoxic conditions following hypoxia (hypoxia-normoxia). This observation is in agreement with that reported for adult white sturgeon at 15° C and consistent with the hypothesis that white sturgeon reduce overall energy expenditure during hypoxia to maintain aerobic energy balance (Burggren & Randall 1978). This is, however, inconsistent with the response to hypoxic stress exhibited by Siberian sturgeon. When subjected to acute, severe hypoxia (10 torr PO_2) and slow-onset, graded hypoxia (PwO_2 = 60, 40, and 20 torr) Siberian sturgeon do not reduce MO_2 and following the return to normoxia, increase oxygen consumption rate (Nonnotte et al. 1993, Maxime et al. 1995). In Siberian sturgeon, the maintenance of energy expenditure during hypoxia is

supported anaerobically and this is evidenced by a metabolic acidosis (increases in plasma lactic acid) and an increase in MO_2 (repayment of an O_2 debt) following the return to normoxic conditions (Nonnotte et al. 1993, Maxime et al. 1995). This distinctly different pattern, compared with the white sturgeon, may stem from habitat-related differences in the Siberian sturgeon's juvenile life history (Ruban & Sokolov 1987, McDowall 1988).

Conditions under which metabolic rate measurements are conducted, may affect fish and their responses to hypoxia. For example, Ruer et al. (1987) studied the effects of high stocking density (3, 7, or 11 sturgeon per respirometer) on MO_2 in white sturgeon during normoxia (water $PO_2 > 130$ torr) and hypoxia (water $PO_2 = 80–100$ torr; 18° C), and they reported no differences in MO_2 and swimming activity between normoxic and hypoxic fish. In their study however, the effect of keeping the fish in a group in the respirometer may have been an 'excitatory' stimulus that may have resulted in a general stress response (increased mutual contact between fish). The stress response would include increases in circulating catecholamines and corticosteroids, and typically, result in an increased oxygen requirement (Mazeaud & Mazeaud 1981, Randall & Taylor 1991, Randall & Perry 1992). Khakimullin (1988) reported that juvenile Siberian sturgeon decreased MO_2 when the number of fish in a respirometer increased, presumably the result of a decrease in locomotory activity associated with the increase in the number of mutual contacts between fish. Additionally, the MO_2 of juvenile Siberian sturgeon did not decrease when the respirometer volume increased in proportion to the number of fish. Ruer et al. (1987) may not have been able to resolve a hypometabolic response to hypoxia due to 'excitement' of the fish in the crowded respirometers. In a different study, McKenzie et al. (1995) demonstrated that the influence of diet on swimming activity and MO_2 can be substantial. In part of their study, two groups of Adriatic sturgeon were maintained on commercial diets and exposed to hypoxic conditions ($PwO_2 = 50–80$ torr; 23° C). In one group, the food was enriched with supplemental omega-3 long-chain polyunsaturated fatty acids (LCPUFA) and the food of the other group was enriched with saturated fatty acids (SFA). During hypoxia, Adriatic sturgeon that received the LCPUFA did not reduce MO_2 or swimming activity. Compared to the fish that received only the SFA in their diet, the fish fed LCPUFA were more tolerant to hypoxia.

In conclusion, we have found that juvenile white sturgeon reduce oxygen consumption rate during exposure to hypoxia. They are oxyconformers and we have demonstrated that the reduced MO_2 during hypoxia, may be achieved in part, by significant reductions in volitional swimming activity. Reducing overall energy costs may increase survival of juvenile white sturgeon trapped in extensive and shallow, hypoxic pools or sloughs.

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